Systems paleobiology

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ABSTRACT

Systems paleobiology seeks to interpret the history of life within the framework of Earth's environmental history, using physiology as the conceptual bridge between paleontological and geochemical datasets. In some cases, physiological performance can be estimated directly and quantitatively from fossils – this is commonly the case for vascular plant remains. In other instances, statistical inferences about physiology can be made on the basis of phylogenetic relationships. Examples from research in paleobotany, marine micropaleontology, and invertebrate paleontology illustrate how physiological observations, experiments and models can link biological radiations and extinctions to both long term environmental trajectories and transient perturbations to the Earth system. The systems approach also provides a template for evaluating the habitability of other planets, not least the ancient surface of Mars. Expanding physiological research motivated by concerns about our environmental future provides an increasing diversity of tools for understanding the relationship between Earth and life through time. The geologic record, in turn, provides critical input to research on contemporary global change.

INTRODUCTION

In universities and medical schools around the world, systems biology has emerged as a critical focus for 21st century research in the life sciences. As a discipline, systems biology reflects the maturation of molecular biology from its early concentration on single genes and their products to the realization that it is the *interaction* of genes and their products that determines the structure and function of organisms. Over the past decade, the Earth sciences have traveled a comparable path, recognizing that the physical and biological Earth are not separate entities but rather interacting components of an integrated Earth system. A *Web of Science* search for "Earth System" retrieved two papers from 1988, neither of which conforms to current use of this term. The same search for 2011 yielded 237 citations. A comparable search of CSA Illumina (Georef) yielded 87 hits for the entire decade of 1980-1990 versus 746 for 2011 alone, an increase in publication rate of two orders of magnitude.

Paleontology has been affected by this disciplinary shift, as more and more paleontologists strive to interpret the fossil record within the context of Earth's dynamic planetary history. Indeed, environmental history provides a necessary framework for understanding the history of life. For this reason, and with an admiring wink toward systems biology, I've come to think of the integrated history of Earth and life as "systems paleobiology." We can use the fossil record, illuminated by comparative biology, to reconstruct a narrative history of life. And, increasingly, geochemical analyses of sedimentary rocks are revealing a history of both long term environmental change and transient perturbations to the Earth system. Biological and environmental history can, in turn, be linked by stratigraphic correlation, but to

interpret correlation in terms of causal mechanisms, we need a bridging concept. Here I argue that *physiology* provides the necessary bridge.

Physiology makes intuitive sense as the conceptual glue between physical and biological history because it provides the proximal interface between life and environment (e.g., Knoll et al., 2007a). But, can we know enough about the physiological properties of extinct organisms to constrain interpretations of evolutionary pattern and process? Obviously, there are aspects of physiology that can't be reconstructed with confidence – optimal growth temperature, for example, or the oxygen-binding capacity of hemoglobins in a Paleozoic invertebrate. That said, there are environmentally important aspects of physiological performance that can be estimated from fossils, and these provide important and underexploited avenues for systems paleobiological research.

In some organisms – as discussed, below, vascular plants provide a particularly good example – important features of physiology can be read with confidence from fossils for the simple reason that physiological performance is strongly biophysical in nature and, therefore, can be inferred from preserved anatomy and morphology. In other organisms, physiological traits can be inferred from the phylogenetic placement of fossils. If, for example, all veneroid bivalves have comparable physiological mechanisms of shell formation, then the recognition that a fossil belongs to the Veneridae directly informs interpretation of its skeletal physiology. Comparative biology shows that individual species may depart from a phylogenetically-shared physiological norm (e.g., Widdicombe and Spicer, 2008), but what the fossil record provides is actually a statistical digest of biological responses to environmental change within and between clades (Knoll and Fischer, 2011). Thus, it may be impossible to determine why one coral species survived end-Triassic environmental perturbation while another didn't, but perfectly feasible to

draw inferences from the observation that, on average, corals and mollusks responded differently to end-Triassic events.

A compelling argument can be made that physiology has long informed interpretations of Precambrian microbial evolution (e.g., Knoll et al., 2012), especially in the case of isotopic biogeochemistry, where laboratory experiments guide the interpretation of observed fractionations (e.g., Thode et al., 1961; Farquhar et al., 1989; Habicht et al., 2002; Sim et al., 2011). Here, however, the focus is mainly on Ediacaran and Phanerozoic evolution, where the advantages of a physiological perspective have more recently come into sharp focus.

PHYSIOLOGICAL INFERENCE FROM PLANT FOSSILS

In 1884, the Russian geographer Wladimir Köppen published a climate map of the world (Köppen, republished in 2011) that, with only limited modification, remains in use today (e.g., Kottek et al., 2006; Peel et al. 2007). One might ask how much data on temperature and rainfall was available in the late nineteenth century for places like the upper Amazon basin or the Hindu Kush, and the answer, not surprisingly, is "very little." Köppen's effort captured climate distribution so well because it was, in essence, a vegetation map. The geographic distributions of plants co-vary with climate because they reflect the fine physiological balance between carbon gain and water loss dictated by annual variations in temperate and rainfall (e.g., Venevsky and Veneskaia, 2003; Harrison et al., 2010). To a large extent, this balance is maintained biophysically, with leaf morphology and the distribution of surface openings called stomata governing the uptake of carbon dioxide, and both stomata and water supply from vascular tissues controlling the hydration of photosynthetically active cells. Thus, plant form dictates physiological performance and, in consequence, the environmental distribution of living plants

(e.g., Givnish, 1979). By extension, preserved features of morphology and anatomy can provide insights into the physiological capabilities and environmental tolerances of ancient plants.

If plants co-vary with climate in space, we might also expect them to do so in time, and the use of plant fossils as paleoenvironmental proxies has a long, rich, and, at times, contentious history. Early in the last century, Bailey and Sinnott (1916) noted that the proportional representation of angiosperm species with entire (smooth) versus non-entire (toothed, lobed or incised) leaf margins varies as a function of mean annual temperature (Fig. 1); they were keenly aware that this empirical relationship could illuminate Cenozoic climate history (Bailey and Sinnott, 1915). Insofar as leaf shape reflects the economics of growth, performance and maintenance (Givnish, 1979; Nicotra et al., 2011), it is not surprising that leaf morphology should vary with climate. Continuing research has verified the relationship between leaf margins and mean annual temperature, although quantification of this correspondence depends on geography and (related to this) phylogeny, and is complicated by water availability (Peppe et al., 2011). Several hypotheses have been advanced to account for the observed distribution (e.g., Feild et al, 2005; Royer and Wilf, 2006), but to date empirical observations run ahead of physiological explication.

The close relationship between leaf form and climate has been used to reconstruct continental climates through the last 100 million years. In general, leaf morphology has been used to estimate a single climate parameter at the time and place of deposition -- usually mean annual temperature (e.g., Wolfe, 1971; Greenwood and Wing, 1995), but occasionally mean annual precipitation (Wilf et al., 1998). Single estimate variables of ancient climate can be compromised, however, because the balance between CO_2 gain and water loss reflects the *integration* of temperature and precipitation variables, manifest in transpiration: the loss of water

vapor from open stomata. Multivariate estimates of ancient climate are beginning to provide more nuanced estimates of Cenozoic environmental history (e.g., Peppe et al., 2011).

Paleoclimate has also been estimated on the basis of climatic distributions of the closest living relatives of preserved plant fossils (e.g., Mosbrugger et al., 2005). This method implicitly integrates physiological tolerances, depending critically on the assumption that closeness of phylogenetic relationship provides a good estimate of physiological performance. Expanding research at the interface between phylogeny and ecology suggests that close phylogenetic relationship does indeed predict both niche dimensions (e.g., Smith and Donoghue, 2010) and climatically sensitive physiological traits (e.g., Davis et al., 2010) and does so well, if not perfectly. In general, then, plant physiology provides tools for reconstructing Paleogene and Neogene climatic history from plant fossils. As systems paleo*biologists*, however, we would also like to understand Cenozoic climate change has influenced plant evolution. Examples abound, including the differentiation of a temperate flora rich in herbs from woody ancestors now most common in tropical and subtropical forests (Judd et al., 1994) and the expansion of grasslands in general (Strömberg, 2011) and C_4 grasses in particular as temperature, rainfall and pCO_2 changed through the era (Cerling et al., 1997; Edwards et al., 2010; Osborne and Sack, 2012).

Stomata provide more specific evidence of physiological linkage between plant form and environmental variables, in this case pCO_2. Leaves are covered by cuticle, a waxy coat that retards the loss of water vapor from leaf surfaces. As cuticle is equally effective in blocking the diffusion of CO_2 into leaves, photosynthetic function requires that leaves have openings (the stomata) through which carbon dioxide can reach photosynthetically active cells in the leaf interior. Water vapor escapes from open stomata, and so the potential for leaf dehydration

requires that stomatal opening and closure be regulated physiologically. Beginning in the late 1980s it became clear that the number, size and distribution of stomata vary with pCO_2 via an incompletely understood feedback loop between physiology and development. One might predict from first principles that when pCO_2 is higher, a lower density of stomata will suffice for carbon gain, decreasing water loss. Woodward (1987) carried out an innovative test of this hypothesis, showing that herbarium specimens of leaves collected before the industrial age had a higher stomatal density than samples of the same species found today in same area. Investigations of stomata through the last glacial-interglacial cycle extended this empirical relationship (Beerling et al., 1993), and laboratory experiments have further contributed to the quantification of stomatal index (stomatal density normalized to the size of surrounding epidermal cells) as a proxy for pCO_2 (reviewed in Beerling and Royer, 2001; Konrad et al., 2008). The individualistic responses of plants to experimental changes in ambient CO_2 indicate that the stomatal index is sensitive to phylogeny, habitat, and water supply from vascular tissues (Konrad et al., 2008; Jordan, 2010). Thus, while stomata provide an important focus for systems paleobiology, quantification remains a topic of active research.

As water supply determines the degree to which leaves can afford to lose water by transpiration through open stomata, vascular tissue provides a third point of entry into the relationship between plant evolution and environment. Trees perform a remarkable biophysical feat, lifting water, sometimes for tens of meters, without expending energy. They can accomplish this because the evaporative loss of H_2O from stomata creates a tension that pulls water upward through the plant's vascular tissue. The rate at which water can move through the vascular system depends directly on the size, shape, and porosity of xylem elements (Sperry,

2003; Pittermann, 2010), and as these can be recovered from anatomically preserved plant fossils, paleontologists can generate quantitative models for fluid flow in extinct plants.

Cichan (1986) pioneered paleobotanical estimates of fluid flow in Paleozoic plants, and with a new generation of physiological models, based on experimental data (e.g., Sperry and Hacke, 2004), additional insights into the water relationships of ancient plants have become available. For example, Wilson et al. (2008) modeled fluid flow for the stem-group vascular plant *Medullosa*, a common constituent of overbank habitats in everwet tropical forests of the late Paleozoic Era. Paleobotanists have long understood that medullosans hydrated exceptionally large fronds by means of a relatively modest stem, and Wilson et al. (2008) showed how this was accomplished. The long, wide, and abundantly pitted tracheids of medullosans conducted water at rates more similar to those of vessel-bearing angiosperms than to living gymnosperms, thereby providing the water required by their large fronds (Fig. 2). Medullosan tracheids contributed little to the mechanical strength of the stem and indeed would have been highly vulnerable to implosion and cavitation (the formation of gas bubbles that occlude fluid flow) at times of even moderate transpirational stress. In light of this, the unusual vascular architecture of medullosans can be interpreted as a means of rehydrating cavitated tracheids and providing a redundant (and therefore, physiologically safe) water supply to leaves. It also helps to explain why medullosans, ecologically successful in wet tropical forests, did not expand widely beyond these environments and why their populations dwindled in the face of Permian climatic change (Wilson et al., 2008).

Paleophysiological investigations of fossil plants continue to expand, fueled by novel insights from plant physiology, itself. For example, over the past decade it has become clear that the vascular system is not simply a passive conduit for fluid flow but rather a system that can be regulated actively by the ionic concentration of ascending water (Zwieniecki et al., 2001; Nardini

et al., 2011). It is thought that pectin in cell membranes acts as a hydrogel, expanding and contracting in response to ionic concentration and, thereby, widening or narrowing the pores through which water passes from one cell to the next. This becomes interesting to paleontologists because the degree to which vascular systems respond to changes in ionic concentration appears to correlate with the presence or absence of lignin in primary cell walls, a property that can be determined for well-preserved fossils via X-ray spectroscopy (Boyce et al., 2004). Thus, paleobotanists can explore the active regulation of fluid flow by plants that have been extinct for millions of years.

Increasing research is also documenting the physiological consequences of high vein densities in angiosperm leaves, relative to those of other seed plants and ferns. High vein density reduces the distance between stomata and vascular supply, increasing the photosynthetic capacity of angiosperm leaves (Boyce et al., 2009; Brodribb et al., 2010). Fossil leaves preserve vein density well, and, indeed, document a secular increase in the vein density of early angiosperms. This, in turn, provides new perspective on the radiation of flowering plants into successive habitats through the later Cretaceous Period (Feild et al., 2011). The increased photosynthetic capacity of flowering plants leaves would have been accompanied by increased rates of transpiration, providing a positive feedback to regional climate that may have facilitated the expansion of rainforests (Boyce and Lee, 2010).

This last point highlights the fact that organisms have not simply responded to environmental change through time – they have been active participants in that change. On scales of time and space that vary from trees shading the ground beneath themselves (i.e., niche construction; Odling-Smee et al., 1996) to the permanent consequences of evolving

photoautotrophs for atmospheric O_2 (e.g., Knoll, 2003) and CO_2 (e.g., Berner 2003), physiological processes have fed back onto environmental state throughout evolutionary history.

PHYSIOLOGY AND PHOTOSYNTHESIS IN THE SEA

Paleontologists have long recognized the Mesozoic Era as a time of faunal transition in the oceans. Commonly called the Mesozoic marine revolution (Vermeij, 1977), this interval is characterized by a major increase in energy consumption by marine invertebrates (Finnegan et al., 2011), the radiation of large vertebrates as top predators in the oceans (Benson et al., 2010), and an acceleration of the evolutionary arms race between marine predators and their skeletonized prey (Aberhan et al., 2006). Bambach (1993, 1999) argued convincingly that faunal change was driven from the bottom up by an increase in the resource base of marine communities -- and specifically pointed to enhanced runoff of nutrients and particulate organic matter from terrestrial environments increasingly dominated by flowering plants.

Boyce and Lee (2011) have argued that the nutritional consequences of angiosperm radiation for marine communities would have been too small and too late to explain observed evolutionary changes in the sea, leaving marine photosynthesis, especially by phytoplankton, as a potential source of bottom-up ecosystem transformation. Microfossils, biomarker molecules, and molecular clocks agree that during the Mesozoic Era the principal primary producers in continental shelf waters changed from green algae and cyanobacteria to the modern dominants of coccolithophorids, dinoflagellates and diatoms (CDD algae; Knoll et al., 2007b). The transition began late in the Triassic Period with the radiations of coccolithophorids and photosynthetic dinoflagellates, and expanded during the Cretaceous to include diatoms, the group that dominates export production in the present day oceans (Falkowski et al., 2004).

What factors facilitated the rise of CDD algae after several hundred million years of green algal dominance among eukaryotic phytoplankton? A case can be made that each CDD clade expanded due to individual adaptation, for example the ability of diatoms to store nitrate in intracellular vacuoles (Kooistra et al., 2007). But one might also ask whether *common* features of these groups also underpin their correlated rise to ecological prominence. Phytoplankton distributions in the modern ocean reflect physical and chemical water mass characteristics (Follows et al., 2007). Might, then, long term transitions in seawater chemistry or circulation have facilitated Mesozoic phytoplankton evolution?

Physiology has a role to play in addressing this issue. For example, Quigg et al. (2003, 2011) noted that the CDD algae have a relatively low demand for iron compared to green algae and cyanobacteria. Perhaps, they argued, increasing ventilation of subsurface oceans during the Mesozoic Era diminished the availability of Fe in the photic zone, favoring CDD clades. Ratti et al. (2011) also looked to ecological stoichiometry, but took a different tack. Noting that CDD algae have an S:C ratio higher than that in most green algae and cyanobacteria for which data are available, and recognizing, as well, that seawater sulfate levels increased (albeit not monotonically) from the early Paleozoic to the present day, Ratti et al. hypothesized that greater S availability might additionally or alternatively have facilitated the rise of phytoplankton with relatively high S demand.

Putting this hypothesis to physiological test, Ratti et al. (2011) grew representative green algae, diatoms, coccolithophorids, dinoflagellates and cyanobacteria in synthetic seawater with $[SO_4^{2-}]$ ranging from 1 to 30 mM (in modern seawater, $[SO_4^{2-}]$ = 28 mM) . The green and cyanobacterial cultures showed no growth response to increasing sulfate levels, but the three CDD algae did, at least up to 10 mM, a threshold first exceeded during the late Paleozoic Era

(Fig. 3). In direct competition experiments, diatoms outgrew green algae and cyanobacteria in modern seawater, but green algae grew best under culture conditions thought to approximate Paleozoic seawater. Thus, laboratory tests provide support for the sulfate-facilitation hypothesis.

As Ratti et al. (2011) made clear, this does not, by itself, solve the problem of the Mesozoic phytoplankton revolution. That will require more experiments on a wider diversity of phytoplankton species. It does, however, illustrate how physiological experiments can illuminate geologically-based hypotheses that link phytoplankton evolution and environmental transition.

Whatever combination of environmental and biological factors drove Mesozoic phytoplankton transition, its consequences would have been important for community organization in the oceans. On average, diatoms and dinoflagellates have cell volumes up to several orders of magnitude greater than those of green phytoflagellates and cyanobacteria in the same waters, possibly reflecting size selection associated with grazing or fluctuations in nutrient supply (Cermeno et al., 2011; Edwards et al., 2011). Given the decreasing calculus of energy transfer from one trophic level to the next, packaging nutrients into larger phytoplankton cells could conceivably have resulted in greater resources for top carnivores. That is to say, that the Mesozoic revolution of phytoplankton might have facilitated the Mesozoic marine revolution of animals. As two of the three radiating phytoplankton clades produced biomineralized skeletons, Mesozoic phytoplankton reorganization also had important consequences for the marine carbonate (Ridgwell and Zeebe, 2005) and silica (Maliva et al., 1989) cycles.

The Mesozoic transition was not the first major reorganization of phytoplankton in the oceans. An earlier shift took place late in the Proterozoic Eon when, following some three billion years of bacterial domination, eukaryotes – largely green algae in the phytoplankton (e.g., Kodner et al., 2008) -- became important contributors to marine primary production. Fossils

(Butterfield, 2000), biomarker molecules (Knoll et al., 2007a), and molecular clocks (Parfrey et al., 2011) all indicate that this rise of eukaryotic photoautotrophs to ecological prominence long postdates the acquisition of photosynthesis by nucleated cells. Can physiology help resolve this transition as well?

Beginning with a seminal paper by Canfield (1998), geochemistry has increasingly suggested that for much of the Proterozoic Eon, anoxic water masses commonly lay beneath a moderately oxic surface ocean (Shen et al., 2002, 2003; Canfield et al., 2008; Scott et al., 2008; Arnold et al., 2004; Johnston et al., 2009; Dahl et al., 2011). In places, perhaps especially on highly productive shelves, the oxygen minimum zone sometimes became sulfidic, but ferruginous water masses may have been even more widespread (Planavsky et al., 2011). How might Proterozoic redox structure have affected the composition of phytoplankton in surface waters?

Fixed nitrogen levels would have been low in Proterozoic surface waters: upwelling ammonia would have been oxidized via nitrification and anammox as it reached the oxic-anoxic interface, while denitrification and anammox would have consumed nitrate and nitrite (Anbar and Knoll, 2002; Fennel et al., 2005). In a photic zone with strong N-limitation, physiological advantage would go to species able to fix nitrogen (Schade et al., 2005), namely cyanobacteria and other photosynthetic bacteria. Consistent with this, at times of transient subsurface anoxia, prokaryotic primary producers have episodically re-expanded in Phanerozoic shelf waters (e.g., Grice et al., 2005; Knoll et al., 2007b; Xie et al., 2010; Hays et al. 2012).

The upward penetration of sulfide into the photic zone is documented regionally by biomarker molecules for purple and green photosynthetic bacteria in mid-Proterozoic shales from Australia (Brocks et al., 2005). To the extent that anoxygenic photosynthesis provided a

persistent if small contribution to marine primary production, this could have sustained a series of biogeochemical feedbacks that worked to limit oxygen accumulation in the atmosphere and surface oceans (Johnston et al., 2009). Geochemical data suggest that as late as 750 Ma, anoxic water masses remained common, even in relatively shallow (above storm wave base) environments (Johnston et al., 2010). This, in turn, suggests that low pO_2 (perhaps no more than a few percent of present day values; Gaidos, 2010) persisted until well into the Neoproterozoic Era.

In mid-Proterozoic oceans low nitrogen availability would have influenced the composition of marine phytoplankton, but not necessarily the amount of primary production -- at least insofar as nitrogen fixation by photosynthetic bacteria could have supplied bioavailable N. Anbar and Knoll (2002), however, proposed that nitrogen availability might indeed have limited primary production in the oceans of Earth's middle age, reasoning that Mo, required as a metallic cofactor in functionally efficient nitrogenase (the enzyme complex responsible for biological nitrogen fixation), would have been in short supply. Zerkle et al. (2006) provided a physiological test of this hypothesis, growing N-fixing cyanobacteria in seawater solutions that approximated the amount of Fe and Mo in ancient seawater. They found that even at Mo concentrations estimated for the mid-Proterozoic ocean, supply was sufficient to sustain high rates of nitrogen fixation, although rates of primary production fell by a factor of two relative to experiments under optimal concentrations, possibly due more to Fe limitation than to molybdenum. Thus, Mo availability may have been sufficient to sustain relatively high levels of photosynthesis in Proterozoic oceans (see also Glass et al., 2010). Once again, physiological experiments provide a means of addressing systems paleobiological hypotheses linking biological and environmental history.

Interestingly, Buick (2007) has proposed a different trace metal influence on the Proterozoic nitrogen cycle. Before the late Neoproterozoic oxygenation of deep oceans, copper would have existed at low abundances in seawater (Saito et al., 2003). Copper is an essential metallic cofactor in the enzyme nitric oxide synthase that reduces N_2O to N_2, thereby completing the biological reduction of oxidized nitrogen to nitrogen gas. In the absence of sufficient Cu, Buick reasoned, N_2O would have escaped to the atmosphere, providing an ongoing supply of this potent greenhouse gas that would have helped to keep the Earth free of continental ice sheets for more than a billion years of Proterozoic Earth history.

Both microfossils and biomarker molecules suggest an increasing presence of algae in later Neoproterozoic primary production (Knoll et al., 2006, 2007b; Close et al., 2011). As oxygen pervaded the subsurface ocean, nitrate would have begun to accumulate in seawater and so, for the first time, eukaryotes would have become competitive in the marine phytoplankton. One might expect that Proterozoic lakes with relative shallow bottoms would have become fully oxic long before the ocean did, with nitrate accumulating in the absence of a strong redoxcline. Consistent with this, geochemical analyses of interpreted lacustrine strata of the 1000 Ma Stoer and Torridon groups, northern Scotland, show evidence of an oxic water column (Parnell et al., 2010), while microfossils in the same succession show evidence of relatively abundant and diverse eukaryotic cells (Strother et al., 2010). The Torridonian succession reminds us that while nonmarine environments are commonly out of sight in Proterozoic successions, they should not be out of mind.

The paleontological and biogeochemical tools needed to reconstruct the history of primary production in the oceans have improved markedly over the past decade, as has the capacity to understand the chemical history of marine water masses. Physiological experiments

have a strong potential to elucidate the systems paleobiological interactions between evolving phytoplankton and changing seawater, providing an improved framework for investigations of animal evolution in the oceans.

OXYGEN AND ANIMAL EVOLUTION

Fossils record animal responses to both long term trajectories of environmental change and transient perturbations in the Earth system. Both have provided major foci for paleontological inquiry, and in both cases physiological insights are reshaping research. No long term trajectory has attracted greater interest than the history of oxygen in the atmosphere and oceans, with particular attention to environmental constraints on early animal evolution. The hypothesis that redox history constrained early metazoan evolution goes back more than half a century (e.g., Nursall, 1959; Cloud, 1968) and reflects physiological experiments completed still earlier (Krogh, 1919). In the present day ocean, animals show a strong and predictable pattern of diversity decrease, smaller size, and lower mobility along gradients of decreasing oxygen availability (Rhoads and Morse, 1971; Diaz and Rosenberg, 1995; Levin, 2003). Where O_2 is chronically absent, only a few physiologically specialized animals can live, for example, tiny loriciferans whose mitochondria have evolved into hydrogenosome-like organelles adapted for anaerobic metabolism (Danovaro et al., 2010). Even these species, however, rely indirectly on oxygen as they obtain sterols required for growth by eating cells that synthesize these molecules in overlying oxic waters.

Invertebrate diversity shows only limited effects of hypoxia down to levels of about 2 ml/l (20-25% of surface saturation, commonly used as the threshold of dysoxia), but below that the effects begin to mount, especially below 10% surface saturation (Diaz and Rosenberg, 1995).

Animals in strongly dysoxic waters display a number of physiological adaptations to low oxygen availability, many of which could not be inferred from fossils. In general, however, these faunas are characterized by two features that do preserve in the rocks: small body size and a dearth of feeding modes requiring persistent, active locomotion (Levin, 2003).

As noted in the preceding section, geochemical evidence suggests that for most of the Proterozoic Eon, even the *most* oxygen-rich environments would have been strongly dysoxic, and persistently anoxic water masses were common in the subsurface oceans. Increasingly, geochemical data support the hypothesis that more persistently oxic oceans appeared only during the Ediacaran Period, and mostly after 580-560 Ma (recently reviewed, with new data, by Li et al., 2010, and Johnston et al., in press). This does not, by itself, contradict molecular clock estimates of 800 Ma for the initial diversification of animals (Erwin et al., 2011), but does place constraints on the body plans and feeding modes available to those earliest animals. Neither does the strengthening evidence for Ediacaran redox transition obviate important roles for developmental genetics and ecology in animal diversification (e.g., Butterfield, 2007; Erwin et al., 2011), although many key events of gene diversification must have preceded the late Ediacaran appearance of large bilaterians (Domazet-Lošo et al., 2008), and major effects of active predation really become apparent only during Cambrian diversification (e.g., Bengtson and Conway Morris, 1992; Erwin et al., 2011). What geochemistry does indicate is that the genetic and ecological determinants of early animal evolution were themselves constrained by environment before the later Ediacaran Period. Only as stably oxygen-rich environments spread through the oceans did large, motile bilaterians begin to assume ecological importance (Johnston et al., in press).

Once the Ediacaran state change was complete, did oxygen cease to shape the evolution of animals? Some have postulated that many evolutionary events recorded by Phanerozoic fossils reflect oxygen rise or fall (Berner et al, 2007), while others have argued that perhaps none do (Butterfield, 2009). Unsurprisingly, increasing research favors a position somewhere between these extremes. It isn't easy to track Phanerozoic pO_2, although a number of biogeochemical models estimate its course through time (e.g., Berner, 2006; Bergmann et al., 2004). Leading models differ in detail, but are consistent in suggesting relatively low pO_2 in the early Paleozoic and higher than present oxygen levels late in the era. Mo isotope data corroborate the view that pO_2 may first have risen to something like modern values about 425-400 million years ago (Dahl et al., 2010). Consistent with this, predatory fish greater than one meter in length first spread through the oceans during the Devonian Period. Physiological research on living fish shows that active predators suffer strongly deleterious effects at oxygen levels well above the canonical threshold for dysoxia; pO_2 even half that of present levels would have placed strong constraints on the early Paleozoic evolution of vertebrates as top carnivores (Dahl and Hammarlund, 2011, and references therein).

Most biogeochemical models agree that the Pennsylvanian and Early Permian periods experienced oxygen concentrations higher than today's, and this has been tied to the fossil record of exceptionally large insects. In an arresting paleontological application of physiology, VandenBrooks et al. (2011, see also Harrison et al., 2011) grew phylogenetically disparate insects under conditions of hypoxia, normoxia, and hyperoxia, showing that some but not all insects respond to elevated pO_2 by increasing body size. The clade-specific capacity for increased size at higher pO_2, which mirrors the selective size increase recorded by late Paleozoic

insect fossils, appears to reflect a developmentally modulated change in tracheal investment not unlike the feedback between stomatal density and pCO_2 in leaves.

It has also been proposed that late Permian decline in the diversity of terrestrial vertebrates can be tied to a concomitant decline in pO_2 (Huey and Ward, 2005) and that the origin and increasing size of placental mammals through time reflects a nearly monotonic increase in pO_2 modeled by Berner (2006) for the past 200 million (Falkowski et al., 2005). The latter argument remains in limbo, as other models for Phanerozoic oxygen history suggest that oxygen has not dipped below present day values for the past 200 million years and, indeed, may have been higher than at present during at least part of the Mesozoic Era (Bergmann et al., 2004). This emphasizes the need for new geochemical tools to provide better empirical estimates of pO_2 through Phanerozoic time. Belcher et al.'s (2010) experimental calibration of the constraints placed by fossil charcoal on pO_2 illustrates the way forward

PHYSIOLOGY AND MASS EXTINCTIONS

In addition to its long term trajectory, oxygen shows evidence of transient depletion in subsurface waters during the Phanerozoic Eon. Indeed there seems to be a broad directional change in the susceptibility of subsurface water masses to anoxia, with persistently anoxic oxygen minimum zones in Proterozoic oceans, episodic subsurface anoxia in Paleozoic seas (Berry and Wilde, 1978), a handful of transient anoxic events in the Mesozoic (Jenkyns, 2010), and few if any globally widespread anoxic events during the past 60 million years. Some Phanerozoic episodes of expanded subsurface anoxia correlate with major extinctions. Intriguingly, however, observed patterns of extinction are not those one might predict based on mapped distributions of animal species across oxygen gradients or experimentally determined

energetic requirements (Knoll et al., 2007a). The spread of anoxic waters across shelf seafloor would undoubtedly have produced mass mortality, as it does in seasonally expanding submarine "dead zones" today (Karlson et al., 2002), and sustained over time scales that are geologically resolvable, expanded anoxia would cause extinction. The extinctions, however, would be indiscriminate within a basin, removing essentially all animal species in affected areas, whereas the pattern actually documented across extinction horizons is one of selective extinction and survival. Extinctions associated stratigraphically with expanded anoxia show a common pattern of selectivity, with the highest proportional loss of taxa among hypercalcifying animals and greatest rates of survival among clades with actively motile species (e.g., Knoll et al., 2007a; Simpson and Kiessling, 2011; Clapham and Payne, 2011). This suggests that if subsurface anoxia played a role in mass extinction selectivity, it was not primarily through asphyxiation (see also Winguth and Winguth, 2012).

When first proposed in 1996, the hypothesis that CO_2 rather than O_2 determined observed patterns of end-Permian mass extinction (Knoll et al., 1996) was received politely at best. Since that time, however, the increasingly resolved correlation between massive volcanism and the extinction event has provided a mechanism for the rapid increase in pCO_2 required for this gas to have deleterious physiological effects. Moreover, growing awareness of present day ocean acidification and its potential consequences for the marine biota (Gattuso and Hansson, 2011) has focused paleontological interest on rapid CO_2 increase as an agent in a number of extinction events (Kiessling and Simpson, 2011).

Much of this interest has focused on the consequences of ocean acidification for the formation of $CaCO_3$ skeletons. Beginning with experiments on coccolith formation by Riebesell et al. (2000), research on pH and skeleton formation has expanded to include phylogenetically

diverse marine animals and protists. As shown clearly by Ries and colleagues, organismic responses to imposed carbon dioxide are neither linear (Ries et al., 2009) nor uniform (Ries et al., 2010). They are, however, consistent with the hypothesis that hypercalcifiers, organisms that deposit large volumes of skeletal carbonate but have only limited physiological ability to buffer the fluids from which they precipitate their skeletons, are differentially vulnerable to the deleterious effects of ocean acidification. This pattern is consistent with the pattern of selective extinction observed at the Permo-Triassic boundary (Fig. 4; Knoll et al., 2007a) and several other times of extinction (Kiessling and Simpson, 2011).

Modeling indicates that the doubling time for atmospheric CO_2 must be about 10,000 years or less to overwhelm Earth's capacity to buffer seawater pH and so decrease Ω, the degree of saturation with respect to calcite or aragonite (e.g., Hönisch et al., 2012). It is the effect of saturation state on skeletonization that has that has occupied center stage in many studies of ocean acidification. Independent of Ω, however, hypercapnia, or high internal CO_2, can have systemic effects on physiological performance, among other things, influencing oxygen transport, growth rate and fecundity (e.g., Pörtner, 2008; Melzner et al., 2009; chapters in Gattuso and Hansson, 2011). The observation that diverse marine invertebrates thrived in Early Paleozoic oceans beneath a CO_2-rich atmosphere tells us that here, too, rate must be important. The rate at which populations can adapt genetically to hypercapnic stress is poorly known and probably quite variable, but, in general the faster the change, the lower the probability that populations will adapt successfully. Rapidly increasing pCO_2 will also fosterglobal warming, with extinction rates expected to peak when rates of climatic change exceed the capacity of populations to adapt or migrate.

In the integrated Earth system, warming induced by rapid injection of CO_2 into the atmosphere should increase rates of continental weathering, enhancing nutrient delivery to oceans, while decreasing the capacity of downwelling water masses to transport oxygen into the subsurface ocean (e.g., Winguth and Winguth, 2012). While anoxia, ocean acidification and global warming have all been implicated individually in end-Permian extinction, experiments show that their physiological effects are synergistic (e.g., Pörtner, 2008; Melzner et al., 2009; chapters in Gattuso and Hansson, 2011). Melzner et al. (2009) summarized this burgeoning literature concisely, noting that more tolerant taxa are characterized by high metabolic rates and high rates of mobility – pretty much what is observed in ancient extinctions linked to rapid CO_2 increase (Fig. 4; Knoll et al., 2007a; Kiessling and Simpson, 2011).

This brings us back to the question of oxygen. As noted at the beginning of this section, subsurface anoxia is associated with some past extinctions, including the early Cambrian demise of archaeocyathids, late Devonian reef collapse, the end-Permian mass extinction, and major extinctions in the late Triassic Period. Is oxygen depletion simply a non-discriminating correlate of CO_2 injection when hypercalcifiers disappear, or does subsurface anoxia contribute to the stresses that selectively doom these organisms? Higgins et al. (2009) developed a model of the marine carbonate system in which they showed that the expansion of subsurface anoxia fosters anaerobic respiration pathways whose product is HCO_3^- rather than CO_2, resulting in deep waters that are less undersaturated with respect to calcite and aragonite than today's, but also surface waters that are less *oversaturated*. This suggests that expanding subsurface anoxia should affect the ability of shallow marine hypercalcifiers to make skeletons much in the way that ocean acidification does, but on times scales that can run to millions of years (further

modeled by Fischer, in Knoll and Fischer, 2011). Thus, widespread subsurface anoxia may have joined ocean acidification in a one-two punch at the end of the Permian Period and, more broadly, may help to explain the episodic collapse of metazoan reefs through time, as well as the prolonged paucity of hypercalcifiers in later Cambrian and Early Triassic oceans (Pruss et al., 2010; Gill et al., 2011; Knoll and Fischer, 2011).

Clearly, then, physiology helps us to understand how and why animals have responded through time to both long term and transient changes to the Earth system. Accelerating physiological research motivated by concerns for the future provide important insights into our understanding of the past – and *vice versa*.

SYSTEMS ASTROPALEOBIOLOGY

A final exercise in systems paleobiology looks upward. We live at a remarkable moment in human history, when longstanding questions about life in the universe can, for the first time, be addressed through observation and exploration. Both because it is relatively nearby and because remote sensing early on showed its surface to be sculpted by fluid flow, Mars has become a principal focus for astrobiological research. We don't know whether Mars ever harbored life, but with each successive mission, we learn more about the environmental history of our planetary neighbor. Adopting the systems approach, we can use known environmental history and the empirically determined physiological tolerances of terrestrial organisms to constrain speculation about possible biological history.

Liquid water is not stable on the present day surface of Mars, but numerous observations indicate that water once flowed across the martian surface and interacted chemically with its

basaltic crust. Geomorphologic evidence includes branched channel systems, outwash plains, deltas, and paleolakes (Carr, 2007; Fasett and Head, 2011), whereas remotely sensed (Bibring et al. 2006; Ehlmann et al, 2011) and ground-based (Squyres et al., 2004, 2011; McLennan et al., 2005) geochemical observations identify clay minerals and salts that record both chemical weathering and ionic transport. Additional compounds might provide biofriendly media under some circumstances, but on Mars water would probably have been required for the emergence of life, as it was on Earth. In the past, water clearly flowed on Mars, but merely observing that it was once present is not sufficient to draw inferences about habitability. We need to know something about the properties and duration of surface water, and this is where physiology assumes importance.

The "ancient mariner's dilemma" illustrates the issue. In Samuel Taylor Coleridge's famous poem "The Rime of the Ancient Mariner," a grizzled sailor lies adrift in a boat, surrounded by water but dying of thirst:

> *Water, water, every where,*
> *And all the boards did shrink;*
> *Water, water, every where,*
> *Nor any drop to drink.*

Why is the mariner dying? Coleridge insists that it is because he killed an albatross, but physiologists know it is because humans cannot tolerate water with the salinity (more properly, water activity = a_w) of seawater. Indeed, all species on Earth, whether animal, plant, fungal, or bacterial, have an empirically observable lower limit to the water activity they can tolerate.

This becomes relevant to Mars because the water activity of the fluids from which martian salts precipitated can be calculated using thermodynamics, if we can make reasonable assumptions about the ionic composition of parent fluids (Tosca et al., 2008). Mg-sulfates

identified at Meridiani Planum, for example, conservatively suggest a water activity of about 0.78 at their time of formation. That is a physiologically daunting figure, only slightly above the a_w for seawater saturated with respect to NaCl. Few terrestrial organisms can tolerate this water activity, but it gets worse -- sodium chlorides deposited from martian waters as late stage evaporites at Meridian Planum and elsewhere record water activities below any known to support terrestrial life (Fig. 5; Tosca et al., 2008).

Clearly the brines from which martian salts precipitated evolved from more dilute solution, which might, themselves, have been habitable, and, indeed, gypsum veins recently discovered along the margin of Endeavour crater likely precipitated from relatively dilute groundwater (Squyres et al., 2011). The fate of these waters, however, was inevitably to evaporate, and at Meridinai Planum, microscopic images show little petrographic evidence for repeated wetting and drying. It appears that water pervaded the Meridiani Planum surface, left, and pretty much stayed gone. The persistence on Mars of jarosite, opaline silica, smectites and other minerals that are unstable in the continuing presence of water further suggests that many parts of the martian surface have seen very little water since these minerals formed an estimated three billion or more years ago (Tosca and Knoll, 2009).

This doesn't necessarily mean that Mars has always had a lifeless surface, but it does suggest that if the martian surface were ever habitable, it was during a relatively limited span of time early in martian history. (Speculation about subsurface life is less easily constrained.) One might argue that it is inappropriate to use terrestrial life as a physiological yardstick for Mars, as life there might have evolved along a different path. Games without rules have many possible outcomes, and so, in the absence of any alternative examples, it makes sense to be guided by the life we know. Regardless of evolutionary origin and molecular makeup, however, life might

have been compromised in brines like those at Meridian Planum due to high concentrations of chaotropic anions that disrupt the structure of proteins and other macromolecules (Zhang and Cramer, 2006; Williams and Hallworth,2009).

In the end, questions about life on Mars must be answered empirically, but the systems paleobiological perspective can help to constrain speculation and identify the most promising targets for those precious opportunities when rovers encounter the martian surface.

CONCLUSIONS

In this essay, I have touched on issues that range from fluid flow in ancient plants to the persistence of water on other planets. Again and again in the geologic record, the stratigraphic correlation of paleobiological and paleonvironmental data suggests a causal relationship between evolution and environmental change. And in numerous cases, our expanding understanding of physiology, rooted in experiments and modeling, suggests means of testing correlation-based hypotheses. At present, it is possible to see the way forward, although answers may remain elusive. A decade from now, I suspect that a new appreciation of the evolutionary past will be within our grasp, bolstered in no small part by physiological research aimed at understanding the 21st century and beyond. At the same time, continuing efforts to understand the biological consequences of current global change will draw increasingly on Earth history. Whether our research looks toward the past or the future, Systems Paleobiology will play an important role in understanding how the Earth system works.

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FIGURE CAPTIONS

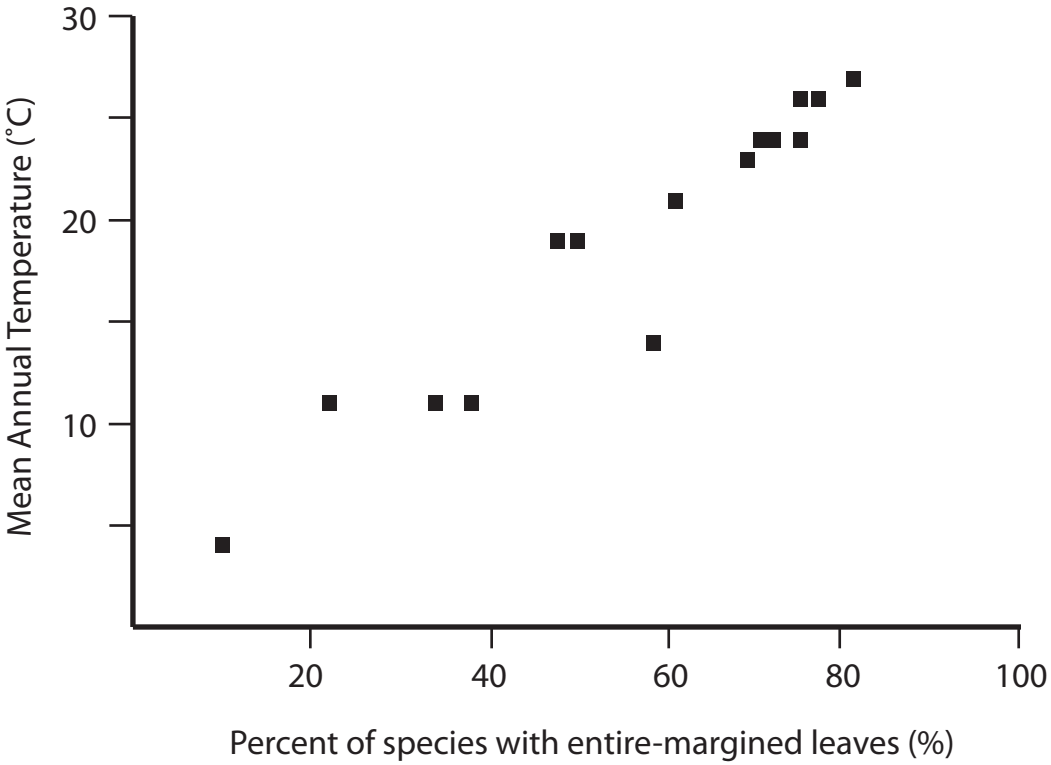
Figure 1. Leaf shape varies systematically as a function of climate, as shown by this plot of the proportional representation of entire-margined species and mean annual temperature (data from Wolfe, 1971).

Figure 2. The rate at which water can be conducted upward through the stem is related to conductivity of individual xylem elements (specific conductivity, or K_{sp}). The plot shows modeled K_{sp} for a variety of living and Paleozoic seed plants (data from Wilson and Knoll, 2010). Living gymnosperms (blue) have relatively small, thick-walled tracheids that conduct water at low rates, whereas angiosperms (red) commonly have vessels with a high K_{sp}. Pennsylvanian seed plants (black) included the conifer-like *Cordaites*, with low per tracheid conductivity, but also genera such as *Lyginopteris*, *Callistophyton* and, especially, *Medullosa* that had K_{sp} intermediate between those of modern gymnosperms and angiosperms. Indeed, the large, porous conducting cells of *Medullosa* had a specific conductivity matched only by vessel-bearing flowering plants.

Figure 3. Growth rates of four phylogenetically distinct algal populations in synthetic sweater with sulfate contents from 1 to 30 mM (slightly above the modern oceans); redrawn from Ratti et al., 2011). Specific growth rate, μ = proportional increase in biomass per day during exponential growth phase. The green alga *Tetraselmis suecica* (in green) shows no systematic effect of increasing [SO_4^{2-}], but the CDD algae (in orange) -- the diatom *Thalassiosira weissflogii*, the coocolithophorid *Emiliania huxleyi* and the dinoflagellate *Protoceratium reticulatum* -- do (the latter two significantly) up to 10 mM.

Figure 4. Selectivity during the end-Permian mass extinction, as a function of skeletal physiology (from Knoll and Fischer, 2011). Hypercalcifiers (left) show a high proportion of genus extinction, as do low activity clades such and crinoids and brachiopods, thought on the basis of physiological experiments to be vulnerable to ocean acidification (Barry et al., 2011). Genera with little or no reliance on calcium carbonate skeletons (right) mostly survived the extinction event, while genera with carbonate skeletons but relatively strong physiological control over the fluids from which skeletal carbonate is precipitated show intermediate levels of extinction.

Figure 5: As water evaporates from solutions of known ionic composition, water activity can be calculated for the point at which specific minerals precipitate. The blue line depicts seawater evaporation on Earth; the red line shows an evaporation sequence on Mars, with ionic composition based on the experimental dissolution of basalts under martian conditions and the observed sedimentary record at Meridiani Planum (redrawn from Tosca et al., 2008).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20
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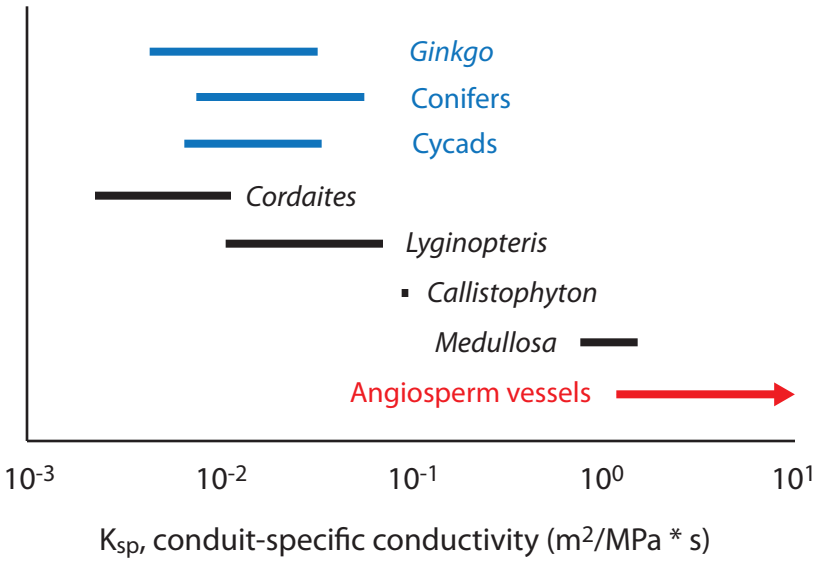
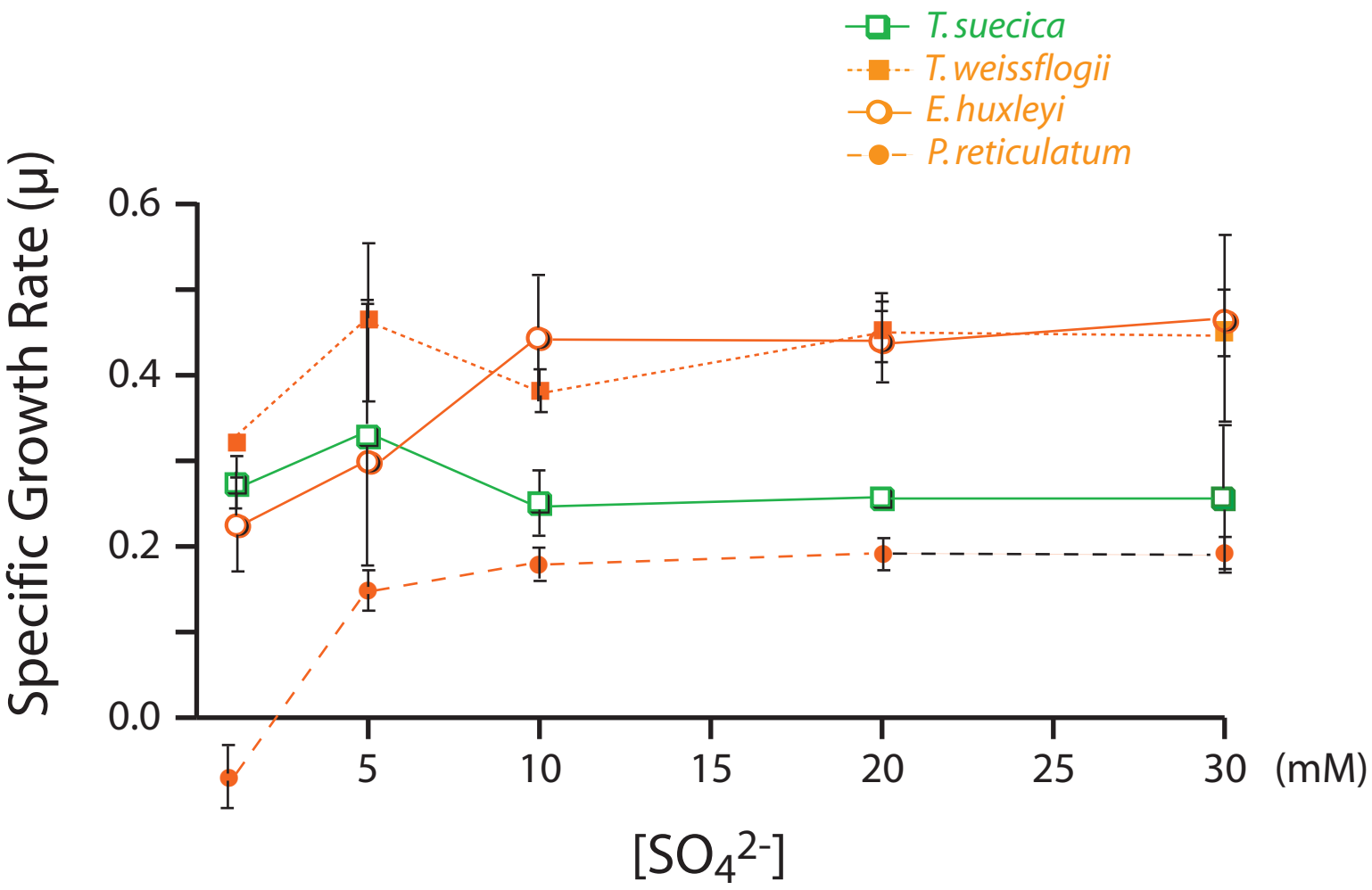
Mean Annual Temperature (°C)
20
40
60
80
100
Percent of species with entire-margined leaves (%)


Ginkgo
Conifers
Cycads
Cordaites
Lyginopteris
Callistophyton
Medullosa
Angiosperm vessels
10-3
10-2
10-1
100
101
Ksp, conduit-specific conductivity (m2/MPa * s)


T. suecica
T. weissflogii
E. huxleyi
P. reticulatum
Specific Growth Rate (μ)
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0.2
0.0
5
10
15
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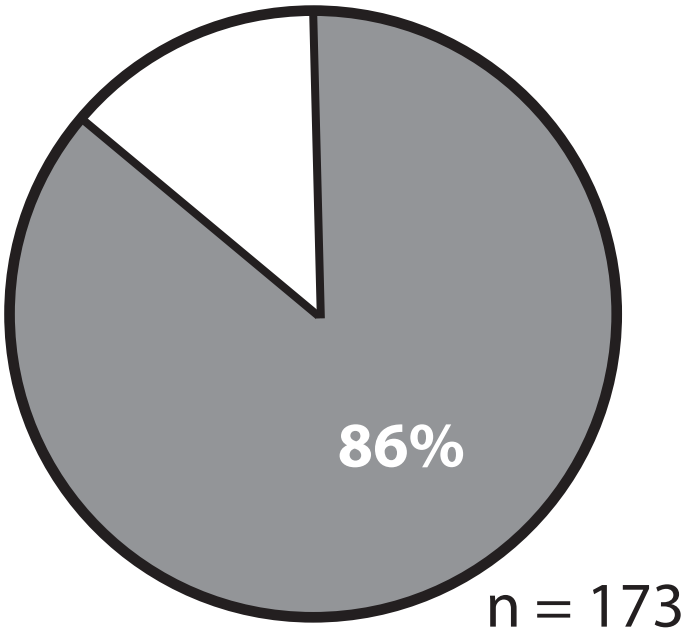
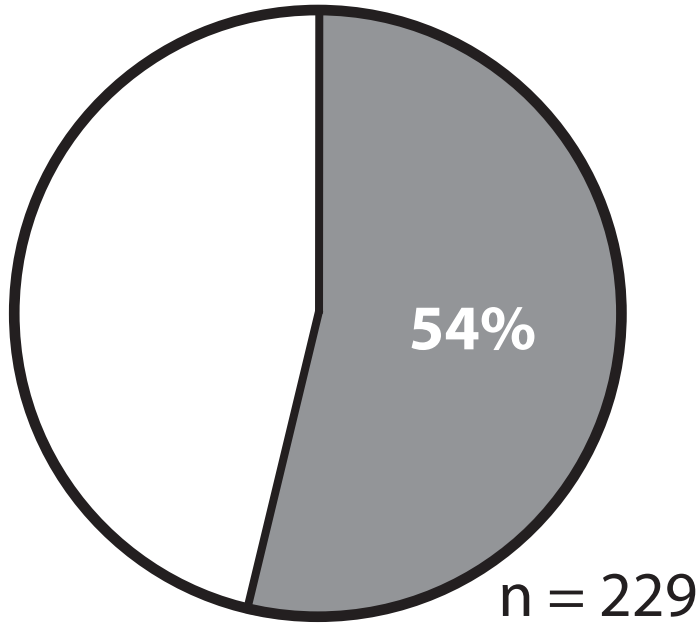
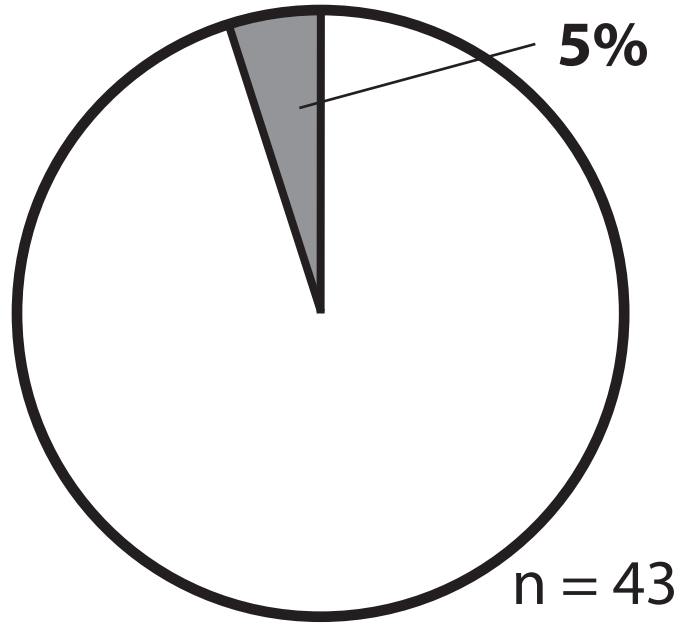
25
30
(mM)
[SO4 2-]







Heavy $CaCO_3$ skeleton (low metabolic rate)

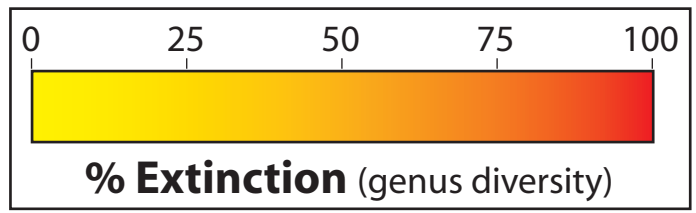
- Rugosa
- Stenolaemata
- Rhynchonelliform brachiopods
  - -Orthida
  - -Strophomenida
  - -Spiriferida
  - -Rhynchonellida
  - -Terebratulida
- Acrotretida
- Crinoidea

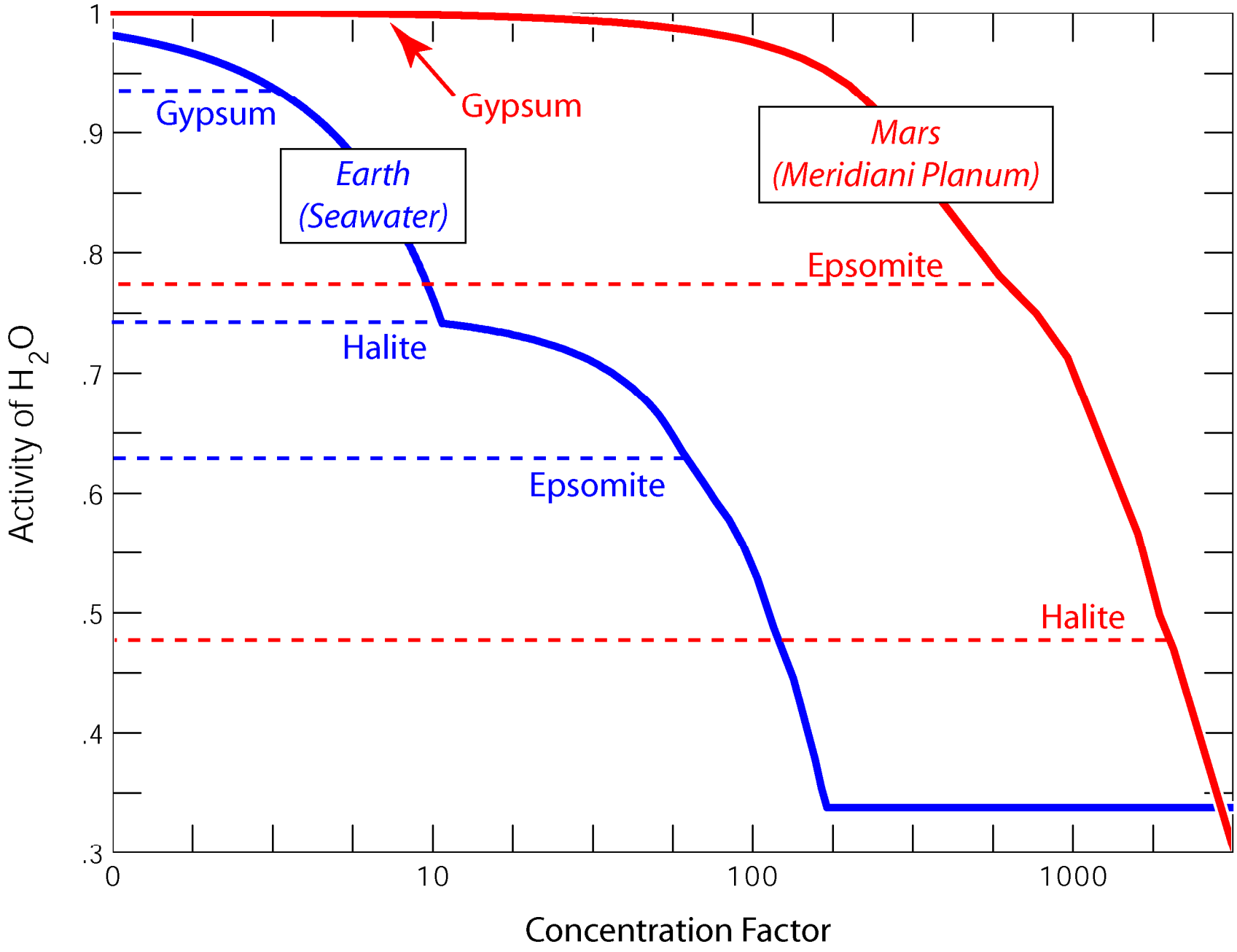
Moderate $CaCO_3$ skeleton (high metabolic rate)

- Gastropoda
- Bivalvia
  - -Infaunal burrowers
  - -Epifaunal, attached
- Nautiloidea
- Ammonoidea
- Ostracoda
- Malacostraca
- Echinoidea

Little or no $CaCO_3$ skeleton

- Ctenostomata
- Lingulida
- Polychaeta
- Holothuroidea
- Conodontophorida
- Chondrichthyes




1
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Activity of H_2O
0
10
100
1000
Concentration Factor
Gypsum
Gypsum
Earth
(Seawater)
Halite
Epsomite
Mars
(Meridiani Planum)
Epsomite
Halite